

THE PRESENT STATUS OF THE THEORY OF EVOLUTION

By GEORGE GAYLORD SIMPSON

Harvard University and the University of Arizona, U.S.A.

Lecture delivered on 17 September, 1968, under the joint auspices of the Royal Society of Victoria and the University of Melbourne

Fact, Theory, Philosophy, and Darwin

In order to consider the status of evolutionary theory, it is good first of all to specify what is meant by 'the theory' or, more generally, 'a theory'. Ill-instructed people in the United States—and I find that this is sometimes true also in Australia—have been known to say, 'Evolution is not a fact; it is only a theory'. The intended implication is that a fact is something indubitably true while a theory is a mere guess.

Rigidly tenable definitions of fact and theory are difficult to come by, and their subtleties could be considered at such length as to preclude grappling with our intended subject. For present purposes it suffices to consider facts as things reasonably established by the observations, and in the opinions, of those qualified to judge, and to consider theories not as guesses or second-class facts but as proposed and confidently supported explanations of facts thus defined.

In any discussion of evolution it is wise to hark back to Darwin. In Darwin's triple accomplishment we do find not only exemplifications of fact and theory appropriate for the present discussion but also philosophical implications. In the first place Darwin marshalled observations so great in number and indubitable in validity that they could not reasonably be understood in any light other than that of organic evolution. Thus, by the admittedly somewhat special definition that I am using here, Darwin revealed evolution as a fact. At the same time and without forcing a distinction between the two accomplishments, Darwin proposed an explanation of the observations testifying to that fact. In other words, he advanced a theory of evolution. *The Origin of Species* not only showed that evolution did occur but also considered how and why it occurred; the book comprises both fact and theory.

Beyond fact and theory there is still another consideration: the bearing of fact and theory on our understanding of our lives and of the universe in which we live. This is the proper domain of philosophy. Darwin was not an academic philosopher, not always even a conscious one, but his work revolutionized philosophy as much as it did knowledge of and explanation in biology. In spite of his generally non-philosophic attitude, he perceived that this was true and it struck him with awe. Biology finally entered fully into the *natural* sciences. Life was now to be comprehended in wholly naturalistic terms, and the origin of our own selves became a material event requiring, indeed permitting, no supernaturalistic postulate.

Thus we have as early as 1859, and more dimly even before that, the fact, the theory, and the philosophy of evolution. Henceforth I shall take the fact for granted, and I shall not attempt to expand on the philosophy. The field to be considered here is delimited as the theory of evolution. While we recognize that Darwin

laid the sound basis for this field, we also note that he left much to be done. There was ample scope for his successors. Much still remains to be done today, and in turn our successors in evolutionary biology will find—with pleasure, I may say—full opportunity to correct and amplify present knowledge and views.

In this connection it is interesting to consider some of the things which Darwin did not do but about which considerable progress has now been made. Here is a quite incomplete but exemplifying list:

Darwin did not develop a clear concept of what he called 'varieties'. He confused varieties as variant individuals within a population, and varieties as variant populations within a species. The two are quite distinct and have importantly different evolutionary roles.

Oddly enough, in the book called *The Origin of Species* Darwin did not explain the origin of species, not, at least, in the sense usually given to the term 'speciation'. Here, too, a distinction must be made between two quite distinct phenomena. A specific population may change so markedly that it evolves into something different, a new descendant species. Most of Darwin's discussion, and the most successful parts of it, related to that aspect of evolution. On the other hand, a specific population may split into two (or more) distinct and separate populations each of which evolves into a species. That is speciation strictly speaking, or the origin of species in common modern usage. Darwin was aware of this aspect as well, but his grasp of it was less clear and his treatment of it less successful.

In Darwin's day no clear demonstration of evolution in action had been achieved. The nearest approach was in the development of domesticated animals and plants by artificial selection. The analogy was extremely useful and fully exploited by Darwin, but the relationship to the origin of natural species was not yet really quite clear.

Knowledge of the factual history of life, even now very incomplete, was so fragmentary in Darwin's day that he had to devote more attention to explaining its apparent failure to elucidate evolution than to such elucidation.

Darwin's most important and most successful theoretical contribution concerned natural selection. Nevertheless he did not quite achieve a fully generalized concept of natural selection, on one hand, or cover its full range of detail on the other.

Along with virtually all the biologists of his and previous ages, Darwin believed in the inheritance of acquired characters. His general theory was saved by his considering this a comparatively unimportant factor, yet it was a serious flaw in general knowledge of evolution at that time. Neither Darwin nor anyone else in his lifetime correctly identified the sources of organic variation or the nature of heredity.

Heredity

Natural selection requires that individuals within single populations differ, that some of the differences (variations) affect their success in reproduction, and that some such differences be hereditary. Those conditions were understood by Darwin and were known to hold true in natural populations. They suffice to validate the theory of natural selection without knowledge of the origin or nature of variations in heredity. However, it was evident to Darwin and his successors that lack of such knowledge was a serious gap in understanding of the whole evolutionary process. Considerable, although still decidedly incomplete progress in this respect has been one characteristic of 20th century biology.

The basis for such progress is commonly ascribed to Gregor Mendel and dated from his publication in 1865, but such ascription is highly questionable. The actual historical importance of Mendel's work was nil, because in itself it led nowhere.

Its principles were independently discovered some 35 years later and it was the latter discoveries that were effective. Mendel's work was known to his contemporaries, but no one then, and notably not Mendel himself, was able to foresee its possible importance. It probably was not known to Darwin, although this is not quite certain. In any case it would have had little or no significance for Darwinian theory in the context then existing. Mendel devised a quantitative, statistical technique that would much later be instrumental in major advances in genetics. The advance made by Mendel himself with that technique was the discovery that some determinants of heredity are discrete and nonblending even though their effects may be masked by the overriding action of others.

It has commonly been said that the assumption of blending inheritance was a fatal flaw in Darwin's theory of natural selection and that it was corrected by Mendel's discovery. That interpretation involves a whole series of misapprehensions. First, Darwinian selection would operate even if heredity were blending, as long as an appropriate source of new variation existed, and the latter is necessary under any theory of evolution. Second, Darwin did not assume that heredity is truly blending, for his own hypothesis as to heredity, although incorrect, involved discrete genetic elements. Third, Mendel's own work had no influence in this respect because neither Mendel nor anyone else related it to natural selection. Fourth, when in later generations the theory of nonblending inheritance was related to natural selection, it failed to take into account that much of heredity does in fact occur as if it were blending; explanation of that fact was left until still later.

The most important achievement of genetics in the early 20th century was development of the gene theory. The concept of the gene was at first and for some two generations purely operational. The gene was something, of variously guessed but not actually known nature, that does something. The observed something that the unobserved something does is some effect on the development or other functioning of an organism. It was established that many of these effects do depend on material units of some sort, and that most, at least, of such units occur in linear sequence in chromosomes. It was found that they are indeed nonblending and that they can and spontaneously do mutate. Further, their behaviour ruled out the Neo-Lamarckian concept of the inheritance of acquired characters. Inevitably in the early development of gene theory, attention was focused primarily on single genes and single mutations. In fact, even though the genes are discrete, all the elements in the entire genetic system interact. That at last explains why heredity often seems to blend, and it requires consideration of development and evolution in terms much broader and by methods more difficult than those earlier based on single genes.

All those discoveries and inferences provided a thorough genetic underpinning for evolutionary theory. With so much operational knowledge of genetic systems at the appropriate evolutionary levels of individuals, populations, and communities, it actually did not matter much what a gene *is* in precise physico-chemical terms. Nevertheless it was clear that this would be desirable knowledge not only for the biochemist but also for the evolutionist. It would eventually supply a still broader basis for evolutionary theory and still deeper analysis of evolutionary phenomena.

Although identification of individual genes is not yet precise, we do now know in general what chromosomal genes are: they are segments of molecules of deoxyribonucleic acid, or DNA. These remarkable giant molecules have four properties in particular that makes their genetic roles possible:

1. In the appropriate cellular environment they become multiplied; replicas of

themselves are produced. Other cells and other individuals can thus inherit DNA with patterns identical to that in an original or parental cell.

2. Occasionally exact replication at some particular point does not occur; there is then a gene or point or locus mutation. This is a source of new variation in a population. (It is far from being the only source of variation.)

3. DNA molecules incorporate four different chemical bases, which may occur in any proportions and in any sequence. Three of these in succession form a functional unit, called a 'codon'. Four bases taken three at a time can form 64 different combinations, all the possible codons. Since DNA molecules are enormously long, the number of codons in each is great, far into the thousands.

4. With a few possible exceptions, each codon corresponds with or is figuratively a code symbol for an amino acid, and a sequence of codons codes for a molecule composed of amino acids in the same definite sequence, that is, for a particular polypeptide or protein. (The actual control or transfer of information from DNA, usually to a protein acting as an enzyme, is complex and need not concern us here.)

Despite some claims to the contrary, I think it unlikely that chromosomal DNA, constituting the classical genes, contains all the information needed to build and operate an organism. Nevertheless it certainly contains a large and essential part of that information. It is thus legitimate, although figurative, to think of the individual genetic system in the strictest sense as a coded message containing information that is passed on from parent to offspring and from cell to cell. But even if we take that literally, it is only the introduction to a mystery and not the solution.

A code is not a language, and a language is not a message. The messages involved here are extremely long, complex, and precise. The coded sequences are correspondingly extremely improbable, which is a requisite for their maintenance of an enormous amount of information. But chemically, or thermodynamically, each of the 64 possible arrangements of bases in a codon and each of the billions of possible arrangements of codons in a DNA molecule are equally probable. Moreover thermodynamically caused changes of sequence (chemical mutations) tend to destroy any information that may have been coded. In terms of communication theory, they introduce noise. The language of chemistry here is gibberish, and the existence of a complex genetic message cannot possibly be explained at this level. In fact we have to explain not only the origin of the message but also the suppression of purely chemical (or thermodynamic) events that tend constantly to reduce it to gibberish.

Genetics and Evolution

Within the context of this modern knowledge of heredity, evolution may be considered as the origin, modification, and maintenance of genetic messages. The present status of the theory of evolution must be discussed in that light.

The most difficult evolutionary problem, indeed the greatest problem of biology as a whole, is adaptation. Every organism is adapted in structure, physiology, and often behaviour to a particular way of life and to particular environmental factors and associations. That is so obvious in general as to be a banal observation, yet often so intricate in particular as to strike awe. A homely example is always before us: our own hands, obviously *made for* grasping and manipulation. We take them for granted, but they are so complex that they have never been completely described chemically, anatomically, and functionally. Among literally millions of other examples are such mutualisms as the adaptations of yucca plants and yucca moths, the plants requiring the moths for their pollination and propagation, the

moths requiring the plants for the development of their eggs and nourishment of their larvae, plants and animals so constructed and in some sense programmed that they not only can but also must carry out these functions.

For adaptations to evolve there must have been some kind of feedback between organism and environment. (The environment of an organism includes other organisms.) Although the term 'feedback' is new, the idea is old, and this feedback was long and often sought in interaction of individual and environment. That has been considered the Lamarckian error, although to do him justice Lamarck did not fall so far into it as did the Neo-Lamarckians, and to do them justice they ignored a still deeper, quite different error into which Lamarck did fall. A too often neglected fact should be obvious: individuals do not evolve. Only populations evolve. The feedback must be in the population, not in the individual. The Neo-Lamarckians hypothesized a transfer of feedback from individual to population, but they were wrong, as recent genetical knowledge makes final. Darwin correctly placed the whole feedback in the population and discovered its basic mechanism. That was his greatest accomplishment.

Now to follow this up we must think not, or not only, in terms of the individual but in terms of populations. The relevant origins, changes, and preservations are those of gene pools, or better of genetic pools, the sum totals of genetic elements in populations. The following are the causes and kinds of changes that occur in genetic pools:

1. **MUTATION.** Point mutation, now construed as substitution of one base for another in chromosomal DNA, has been mentioned. More broadly, mutation can also be taken to include such other events as duplications, elisions, or reversals of base sequences or genes or changes in numbers of chromosomes, although mutation in this sense is less clearly distinct in principle from recombination. The essential feature of mutations is that they introduce distinctly new variants into a genetic pool.

2. **RECOMBINATION.** Sexual and parasexual processes, usual although not quite universal in organisms, constantly produce new combinations of genetic factors already present in a population. Different combinations of genes within a chromosome, sometimes similar to mutations in effects, arise from crossing-over. Reduction of chromosomes from diploid to haploid sets in meiosis produces stochastic, generally new haploid combinations. Fertilization similarly produces stochastic, generally new diploid combinations. These processes, in themselves, do not change the natures or frequencies of genes in a genetic pool, but they produce prodigious numbers of variant combinations of those genes and hence of variant individuals in a population.

3. **GENETIC MIGRATION.** Sexual and parasexual processes may also involve transfer of genes, or more broadly of any genetic factors, from one population to another. In the recipient population that generally involves introduction of new genetic factors, analogous to mutation, or rise of new combinations of such factors, another kind of recombination, or both.

4. **SAMPLING ERRORS.** This somewhat equivocal term, borrowed from statistical theory, is used to express the fact that even if other things are equal a descendant population generally tends to have frequencies of genetic factors somewhat different from the frequencies in ancestral populations. This phenomenon reaches an extreme when a new population arises from a small number, perhaps only one or two individuals from an ancestral population, for example by dispersal to an isolated island. The founders of the new population certainly will not carry all the ancestral population's genetic combinations and almost certainly not all its gene alleles. At the other

extreme, in a continuously large and fairly panmictic population gene frequencies usually tend to fluctuate but little around a stable mean.

5. NATURAL SELECTION. This factor will be defined and discussed in the next section.

The first three of those five influences changing genetic pools tend to maintain or to increase variation in populations. The fourth commonly tends to decrease variation temporarily. All are important factors in evolution. Indeed, in combination, they are absolute requisites if evolution is to occur at all, for they provide the materials and the basis for evolutionary change. However, none of them is oriented with respect to adaptation. Although not random in an absolute or unlimited sense, they are random or stochastic in the sense of having no connection, in themselves, with origin or maintenance of adaptations. None of them is oriented by feedback from the organism-environment interaction. Evolution under their influence alone would involve adaptation by chance. But adaptations of organisms are so universal and so intricate that their origin or maintenance by chance would be enormously improbable, improbable quite to the point of utter impossibility. There must, then, be a fifth factor that is correlated with adaptation, that does include organism-environment feedback, and that provides an antichance element in the orientation of evolution. That factor is natural selection.

Natural Selection

Once Darwin had pointed it out, the reality of natural selection became obvious. It followed unquestionably from a concatenation of facts none of which can be seriously doubted:

- Natural populations tend to produce more offspring than survive to maturity.
- Individuals in a population differ.
- Some of their differences are hereditary.
- Some hereditary differences affect survival.

Therefore such differences as promote survival will tend to accumulate in a population.

Put in just that way, the principle of natural selection is indubitable, but it is limited in scope and significance. There was considerable force in the criticism that Darwinian selection, with its emphasis on survival in the struggle for existence, was primarily negative and accounted rather for the elimination than for the origin of organic characteristics. Darwin himself did take a broader view, and this has been adopted and greatly clarified since his day. He wrote, 'I use the term struggle for existence in a large and metaphorical sense, including dependence of one being on another, and including (which is more important) not only the life of the individual but success in leaving progeny'.

At present 'success in leaving progeny' is not merely included in the principle of natural selection. It is the whole point. For precision, the following conditions must be made further explicit: the success in question is relative or comparative either within a single population or as between two interacting populations; it involves an average over a considerable period of time in terms of generations of the organisms involved; and the success must have a positive correlation (however slight) with a genetic factor or combination of factors. With those conditions understood, natural selection is defined as *genetically differential reproduction*.

For any given kind of organism a vast number of conditions both external and internal can influence reproduction and thus can have a bearing, positive or negative, on natural selection. The direct influence generally takes one of three forms.

First is mortality, or, conversely, survival selection, which acts by genetically differential failure of individuals to survive through the whole reproductive period. That is the most obvious form of selection and was most emphasized by Darwin and his immediate followers. Second, and in many species at least equally important, is fecundity selection, genetically differential success in leaving descendants. This is a populational phenomenon and is to be measured not within reproductive units in single generations but in populations over periods of several generations. It is also noteworthy that fecundity selection can be influenced, mostly among highly socialized animals, by members of a population that are not themselves actively reproducing, as by workers among ants or helpful grandparents among humans. A third relatively little emphasized form of selection is by age of parenthood. Within a population, parents that begin reproducing at an earlier age will tend to have more descendants at any given time thereafter than parents that begin late. This effect is generally not obvious, because it is often cancelled out by mortality selection or masked by the greater effect of fecundity selection.

Natural selection may further be seen to operate at different biological levels. Action most directly at molecular and nuclear levels is for the most part elimination of gross abnormalities, hence negative and little involved in positive adaptation or evolutionary change. Usual positive action directly involves the phenotype as a whole, and hence indirectly the genetic system as a whole. To think of selection as acting on single genes or to rely on mathematical models so based, as was usual in earlier stages of population genetics, is usually unrealistic. At the organismal and populational levels involved in usual selection, its effects can rarely relate to a single gene. Even at the level of the genes themselves relevant selection rarely acts separately on one gene. Genes are discrete but not isolated; their actions are balanced and integrated by complex interactions. That is true within individuals. In the population, where adaptive feedback occurs, there are further complications. No attempt can here be made to summarize knowledge of these, but a striking example may be mentioned: balanced polymorphism. In this phenomenon, which now appears to be rather widespread, individuals heterozygous at a particular gene locus are selectively favored over homozygous individuals. Because a heterozygous population necessarily produces a certain percentage of homozygous offspring, positive selection on the population in such cases is itself productive of individuals subject to negative selection.

Some misapprehensions about natural selection linger on from Darwin's day, although Darwin himself did not share all of them. One that he sought to correct and yet fostered by the phrase 'survival of the fittest' is that natural selection tends in the direction of individual superiority, of increasing fitness in the vernacular sense. In fact it tends only toward relative success in reproduction. Geneticists have confused the issue by defining fitness as such success, which makes selection as 'survival of the fittest' a banal tautology. It is usually true that fitness in the nontechnical sense of individual adaptation does make for relative success in reproduction of the population. That is why and how natural selection does cause adaptation, but the relationship is indirect and is not invariable.

The same point is further involved in some obscurity in the distinction between natural and artificial selection, another thing not yet absolutely clear in Darwin's pioneering studies. The essential difference is not just that one occurs in nature and the other is conducted by man, but that the sole direct effect of natural selection is a relative reproductive differential under existing conditions while the purpose, and, if successful, result of artificial selection is change in any characteristic other than reproductive differential. Many experiments on selection do not involve

natural selection, because that differential is controlled by the experimenter and not by the experiment. (Such experiments may nevertheless produce genetic information useful in consideration of natural selection and other factors of evolution.) It often happens in plant and animal breeding that natural selection, which occurs willy-nilly in such artificial procedures and not only in nature, eventually runs counter to artificial selection and limits or ends the breeder's progress.

Another point that has required and received clarification since Darwin is the relationship between natural selection and sexual selection. Years elapsed between Darwin's publication of *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* (the full title of his most famous book, first edition in 1859) and that of *The Descent of Man and Selection in Relation to Sex* (1871). It was not merely incidental that the latter book, in which Darwin first overtly discussed human evolution, also included the apparently distinct topic of sexual selection among animals in general. Darwin believed that natural selection favored the fittest as the best adapted. However, he was persuaded that differences among human races are not in themselves adaptive. Hence if an evolutionary explanation was to be given for the origin of those races, he believed that some directive factor other than 'the survival of the fittest', or natural selection in that sense, was needed. That difficulty was probably among the complicated and diverse reasons why Darwin was among the tardiest of the Darwinists to apply his theories to human evolution.

Darwin's proposed solution was that among humans and some other animals, choice is involved in mating and consequent production of offspring. Some individuals appeal more to the eyes (or ears or noses) of members of the opposite sex. They therefore have greater chances of leaving descendants, and their heritable characteristics, although not adaptive in relationship to the environment, will selectively increase in the population. This phenomenon does occur, but it is now considered less general or important and is viewed somewhat differently. For one thing, Darwin's premise has become dubious. It is now believed that many racial characteristics, possibly the majority or even (but somewhat unlikely) all of them are in fact adaptive to regional environmental conditions, taking 'environment' in a broad sense. (In the case of human races, their members no longer live under the conditions to which the races originally became adapted, and determination of the exact nature of the adaptation is correspondingly more difficult.) Further, when sexual selection does occur, its effect is to produce a genetic differential in reproduction within a population, in other words, natural selection. It therefore is not an alternative but simply a special case of natural selection, or one of the very large and varied body of factors that can lead to natural selection under particular conditions.

It is still arguable whether nonadaptive characters arise and persist in the course of evolution, that is, whether variants completely neutral with respect to natural selection occur and continue to lack any selective significance. Oddly enough, it is more likely and is easier to explain that inadaptable characters are involved, that is, that characters adverse or negative to natural selection nevertheless do arise and persist. Definition of that phenomenon depends, however, on taking an unduly narrow view of the whole phenomenon. Such characters are inadaptable only if they are considered in isolation and in a defined and static environmental situation. In balanced polymorphism, previously mentioned, the homozygotes are inadaptable, but they are a necessary outcome of a genetic situation that is over-all adaptive for the population through its production of heterozygotes. More generally, an individual genetic system may have both adaptive and inadaptable, selectively both positive and negative, phenotypic correlates, and selection will act on the algebraic sum

of those correlates, not on each adaptive and inadaptive character separately. If the selective balance is positive, selection will develop or maintain the system even if it includes inadaptive phenotypic characters.

It is further important that maximum adaptation to a fully specified, static environmental situation has a poor evolutionary prognosis. Such adaptation would be equal for all individuals, with minimal or no genetic variation in the population. But no environment is in fact stable in all its details, and change in genetic adaptation can occur only on the basis of pre-existing variation. Thus the idea once held that species normally have a particular 'wild type' representing optimal adaptations for any and all individuals is not valid from the more significant point of view of populations. The optimum for continued existence of a species is almost always a variable and relatively labile population. There is a fact highly pertinent here that is not always sufficiently taken into account by nonpalaeontological evolutionists and that would not have been guessed if the fossil record had not revealed it. The vast majority of species in the history of life have become extinct, extinct by termination without issue and not in the purely nominal sense of extinction by conversion into a new, different species. Here is a vital paradox: natural selection, a process requisite for survival of species, has extinction, non-survival, as its *usual* outcome.

Finally in this extremely summary treatment of natural selection, reference may be made to the previous observation that evolution requires the suppression of purely chemical or thermodynamic events in the genetic system. If strictly chemical processes at the individual and molecular level had, so to speak, been given their head, not merely the majority but the totality of organisms would now be extinct. The answer is again natural selection. Survival of lineages of organisms through geologically significant spans of time demands a measure of adaptive lability, dependent on genetic variability. Nevertheless the overall adaptation of the lineage as a species at any one time requires considerable uniformity in its members. It is usual that extreme phenotypic variants are more subject to early mortality and less fecund than those nearer the population mode, which is therefore usually favored by natural selection. In this role natural selection is a centripetally directional force or a stabilizing or homeostatic mechanism, tending to conserve the existing adaptation of a population, to counteract adaptively unoriented influences such as mutation, and to damp out stochastic fluctuations of the genetic pool. When directional change is occurring under the influence of natural selection, the most extreme variants, even those in the direction of that change, are commonly at a selective disadvantage. Thus the rate of change is moderated by simultaneous stabilizing selection, and the trend is self-braking. The fossil record is replete with examples of long, slow trends. In laboratory experiments with stabilizing selection artificially eliminated, similar changes can be produced at rates sometimes literally millions of times faster. In nature the most common and strongest effect of selection is not for change but for evolutionary homeostasis.

Speciation

Study of the origin of species, taken literally and not so broadly as by Darwin, has involved especially two primary problems and a multitude of secondary ones. There is not time here to discuss any of the secondary problems, interesting and important as they are, but a few words can be devoted to each primary problem.

The first problem is whether evolutionary change, and particularly such change as results in what are recognized as new species, occurs in single steps, by saltation

in a term now somewhat old-fashioned, or gradually. Darwin recognized the existence of saltations, now considered mutations of quite diverse sorts, but held that they are relatively unimportant for the origin of species. He believed that all kinds of evolutionary changes are usually gradual. Discovery that genes are discrete units and that mutations in the broadest sense are discrete events persuaded many early geneticists that such evolutionary events as the origin of species are also normally discontinuous, or occur by noticeably separate steps. That is true in a minority of cases, especially by mutational alterations in chromosome numbers, common only in plants and apparently important only at relatively low levels of evolutionary change.

Beyond that, better knowledge of genotypic and phenotypic variation and abandonment of typological in favor of populational concepts have put the subject on a different and sounder basis. The greater part of phenotypic variation on which natural selection acts occurs in such numerous and small steps as to be effectively continuous. Although completely without knowledge of the molecular substrate, Darwin was right that the usual materials for evolution are small variations. Moreover, regardless of the size of steps possibly involved, the process of change is now seen to be gradual in populational terms when it occurs by shift of parameters of variants in a single continuing biological population and not by instantaneous emergence of a new 'type' outside the parental 'type'. By far the most common course of evolutionary change is gradual in the present sense, and again Darwin's gradualism was correct although he expressed it in different terms and necessarily with less understanding in depth.

The second primary problem for brief consideration here is that of the origin of species in the sense of the splitting of a lineage into two or more. I have already noted that this is one of the few subjects on which Darwin was obscure and confusing. Clarification has come especially from realization that the crucial event is strong limitation or cessation of interbreeding between segments of a population and that such reproductive isolation is generally a cause, not a result, of genetic and phenetic divergence. It has further been determined that such isolation does not normally arise between fully contiguous parts of a population. The usual antecedent is geographic separation, and different species from one ancestral population generally arise in different regions, that is, allopatrically. There are probable exceptions to that rule, and the extent and nature of such exceptions are still subject to debate, sometimes rather heated but of no great importance for the present summary.

A segment of a population that has become geographically segregated does not become a new species *ipso facto* and forthwith. Gradual divergence will inevitably occur if segregation is long-continued. Since this process is gradual, there is no exact point at which the distinction can be unequivocally called specific. In principle, speciation has occurred when the two groups will not interbreed or will do so only to quite limited extent even if they come into contact. In many cases nature has supplied this criterion, but in others its probability must be judged on indirect evidence, especially by the degree of anatomical, physiological, and behavioural divergence. Impediments to interbreeding of groups otherwise in contact with each other are called isolating mechanisms. They are astonishingly varied, and a great deal of ingenious and fascinating research has been devoted to them, especially among vertebrates in which complex behavior is often involved, and among insects. Speciation is finally and irrevocably complete when production of fertile hybrid offspring has become genetically impossible. That stage is finally reached if the relevant populations survive for any great length of time. In spite of the existence

of many interspecific hybrids, they are exceptional, and most natural species are completely isolated genetically.

Some Other Aspects

In considering the present status of the theory of evolution I have dwelt on just a few of the subject's most important aspects. It is further characteristic of the present status that theoretical and other study of evolution is now even more widespread, its aspects even more diverse than ever. In the remaining time I can only exemplify and not exhaustively list other aspects, and the examples can only be mentioned and not amply discussed.

The study of evolution as history, of the actual course followed in the descent and diversification of organisms on earth, has progressed enormously since Darwin's day and is now most energetically pursued. In Australia, for example, where really active students of the subject could have been counted on the fingers of one hand a generation ago, there are now programmes carried out from each capital city and in most of the museums and the increasingly numerous universities. The total effort throughout the world is much more complex and significant than the gathering of primary historical data, intensive and essential as that is. Three major steps or activities are involved:

1. ACQUISITION OF DATA. These and their interpretations are of two kinds, sequential and comparative. Sequential data, provided by fossils and their living successors, show faunal, floral, and phylogenetic changes on a direct time scale. Comparative data, derived from both fossil and recent organisms but mainly the latter and without applicability of a definite time scale, permit inferences as to evolutionary sequences not directly observable as such.

2. STUDY OF EVOLUTIONARY PROCESSES. The processes that act through history and produce evolution are not themselves historical in nature. They are (or at least are postulated to be) immanent features of the universe, unchanging themselves while they cause or influence changes in material organisms. These processes include and are well exemplified by natural selection and speciation, previously discussed.

3. CONFRONTATION OF THE PRECEDING TWO ASPECTS OF STUDY. This is the most important theoretical aspect of the historical study of evolution. It includes the explanation of historical events in terms of known explanatory (that is, theoretical immanent) processes, and on the other hand it checks hypotheses about processes against factual historical data.

In the course of historical and other theoretical studies, many particular kinds of evolutionary change have been specified, described, and at least partially explained. For example there are the related phenomena variously discussed under such terms as 'ecological incompatibility', 'displacement', 'Gause's principle', and others. The principle is that if two sympatric populations compete for any environmental resource that could be wholly utilized by one of them, it will happen either (1) that one population becomes extinct at least in the area of sympatry, or (2) that the populations will evolve in such ways as to make them ecologically more distinct and less competitive. This happens to be an example, by no means unique, of a principle already well-known to Darwin and clearly stated by him but several times 'discovered' and renamed in recent years. Recent discussion has, indeed, supplied better knowledge, experimental evidence, and more complete explanation of the phenomenon. That is also true, for example, of the principle that individual adaptability can be selectively replaced by genetic adaptation. That was stated by Baldwin

and others in the 1890's, but recent 'discovery' has been accompanied by embryological and genetical explanation not earlier possible.

In other instances, mimicry for example, recent students have been well aware that the phenomena were well known in the 19th century but have contributed greatly in the way of new data and extended explanations. It must not be thought, however, that all recent discoveries are merely rediscoveries or that recent study only exemplifies knowledge of principles already known. Genetic homeostasis, mentioned previously, is one of many examples of principles discovery of which is in fact recent.

As evolution is pervasive and involved in all biological phenomena, it follows that all developments in the science of biology have a bearing on evolution. This review will be closed with two exemplifications of that fact, one having to do with developments in methodology and instrumentation, the other with advance in highly specialized knowledge. The first example involves the fact that biology has shared in the increasing quantification of all sciences and availability of electronic computers capable of rapid processing of enormous bodies of quantitative data. Many evolutionary studies cannot usefully be approached in those ways, but many can be and are being. Mathematical models of selective processes and of their interplay with stochastic factors can now be made much more complex and in that respect much more realistic. The zoogeography of islands can be studied with sophisticated quantitative methods taking into account such factors as area, width of barrier, source fauna, ecological diversity, and others. Phenetic similarity among organisms can be represented by measures involving large numbers of characters. It should perhaps be added in a cautionary way that all these and other computer methods, useful as they are, provide only manipulations of data. At one end, specification of the manipulations to be used, and at the other end interpretations and theoretical conclusions still have to be supplied by hand, or rather by human brain.

Finally, it is noted with utmost brevity that the present activity in the field of molecular biology is potentially of great evolutionary interest and value. The rapprochement of molecular and evolutionary biology, fields that were formerly sometimes considered quite distinct or even antagonistic, is now being actively pursued from both sides. There is still considerable misunderstanding and the results so far are relatively few and preliminary, but this is certainly one of the most interesting and probably one of the most promising developments in modern biology.

Bibliography

Citations of authority are not given, but the following brief list of general works in relevant fields may be useful.

- BEADLE, G. & M., 1966. *The language of life*. Garden City; Doubleday.
 DARWIN, C., 1964 [1859]. *On the origin of species*. [Facsimile of the first edition.] Cambridge (U.S.A.); Harvard Univ.
 DOBZHANSKY, TH., 1962. *Mankind evolving*. New Haven; Yale Univ.
 FLORKIN, M., 1966. *A molecular approach to phylogeny*. Amsterdam; Elsevier.
 GRANT, V., 1963. *The origin of adaptations*. New York; Columbia Univ.
 HUXLEY, J. S., 1963. *Evolution: the modern synthesis*. 2nd edition. London; Allen and Unwin.
 JUKES, T. H., 1966. *Molecules and evolution*. New York; Columbia Univ.
 MAYR, E., 1963. *Animal species and evolution*. Cambridge (U.S.A.); Harvard Univ.
 SIMPSON, G. G., 1964. *This view of life*. New York; Harcourt, Brace and World.
 ———, 1967. *The meaning of evolution*. Revised edition. New Haven; Yale Univ.
 ———, 1969. *Biology and man*. New York; Harcourt, Brace and World.
 SIMPSON, G. G., & BECK, W. S., 1969. *Life: an introduction to biology*. Revised & shorter edition. New York; Harcourt, Brace and World.
 TAX, S., ed., 1960. *Evolution after Darwin*. 3 vols. Chicago; Univ. of Chicago.